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SPECIAL FEATURE: SCIENCE FOR OUR NATIONAL PARKS' SECOND CENTURY

Using structural equation modeling to link human activities to wetland ecological integrity

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Abstract. The integrity of wetlands is of global concern. A common approach to evaluating ecological integrity involves bioassessment procedures that quantify the degree to which communities deviate from historical norms. While helpful, bioassessment provides little information about how altered conditions connect to community response. More detailed information is needed for conservation and restoration. We have illustrated an approach to addressing this challenge using structural equation modeling (SEM) and long-term monitoring data from Rocky Mountain National Park (RMNP). Wetlands in RMNP are threatened by a complex history of anthropogenic disturbance including direct alteration of hydrologic regimes; elimination of elk, wolves, and grizzly bears; reintroduction of elk (absent their primary predators); and the extirpation of beaver. More recently, nonnative moose were introduced to the region and have expanded into the park. Bioassessment suggests that up to half of the park's wetlands are not in reference condition. We developed and evaluated a general hypothesis about how human alterations influence wetland integrity and then develop a specific model using RMNP wetlands. Bioassessment revealed three bioindicators that appear to be highly sensitive to human disturbance (HD): (1) conservatism, (2) degree of invasion, and (3) cover of native forbs. SEM analyses suggest several ways human activities have impacted wetland integrity and the landscape of RMNP. First, degradation is highest where the combined effects of all types of direct HD have been the greatest (i.e., there is a general, overall effect). Second, specific HDs appear to create a "mixed-bag" of complex indirect effects, including reduced invasion and increased conservatism, but also reduced native forb cover. Some of these effects are associated with alterations to hydrologic regimes, while others are associated with altered shrub production. Third, landscape features created by historical beaver activity continue to influence wetland integrity years after beavers have abandoned sites via persistent landforms and reduced biomass of tall shrubs. Our model provides a system-level perspective on wetland integrity and provides a context for future evaluations and investigations. It also suggests scientifically supported natural resource management strategies that can assist in the National Park Service mission of maintaining or, when indicated, restoring ecological integrity "unimpaired for future generations."

Key words: beaver; ecological integrity; human disturbance; Special Feature: Science for Our National Parks' Second Century; structural equation modeling; ungulates; wetlands.

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Introduction

Wetlands are globally threatened ecosystems (Tiner 1984, Gibbs 2000)—not a desirable situation given that they are also critical and highly valued habitats, with concentrations of biodiversity and important ecological function (Patten 1998, Bedford 1999, Zedler and Kercher 2005). Protected areas like Rocky Mountain National Park (RMNP) can serve as refuges for comparatively intact wetland ecosystems. Recent management approaches implemented by the U.S. National Park Service (NPS) have focused on science-based management and restoration (i.e., U.S. NPS 2006); however, to date, success has been elusive (Colwell et al. 2012). Threats to wetlands often transcend the boundaries of even large wilderness parks (Lee et al. 2015), and inertia from historical degradation that occurred prior to NPS ownership is high. All of these factors have often led to reduced functionality and loss of wetland integrity in parks like RMNP (Davis and Ogden 1994, Baron et al. 2000, Wolf et al. 2007).

Significant work has explored relationships between wetland condition and its drivers (i.e., Winter 1988, Brinson 1993, Zedler 2000, McLaughlin and Cohen 2013, Garssen et al. 2015). Several recent efforts have developed quantitative methods for estimating wetland ecological integrity (Schoolmaster et al. 2013*a*, *b*, Miller et al. 2016), building on a rich literature from other systems (i.e., Karr 1991, Hawkins et al. 2000). In some cases, integrity is defined and estimated using theoretical knowledge of key characteristics and processes operating in an ecosystem. In other approaches, indices of human disturbance (HD) estimate ecological responses sensitive to disturbance that are then combined in indices of departure from a defined reference condition (e.g., the index of biotic integrity; Karr and Kerans 1992, Stoddard et al. 2006, Mack 2007). Scoring these indices or "bioassessment" (Barbour et al. 1999) is relative to general HD gradients with no mechanistic or causal connection made to the actual stressors that degrade integrity at a site. While bioassessment provides useful information, especially for classifying or prioritizing potential regulatory actions (U.S. EPA 2015), it generally does not provide actionable information that resource managers may use "on the ground." In part due to these shortcomings, the NPS Inventory and Monitoring (I&M) Program was established in 1998 to provide ongoing evaluation of status and trends in "vital signs" of important park natural resources in support of science-based management (Fancy et al. 2009). Long-term monitoring by the I&M Program provides rich data sets that document ecological condition (Tierney et al. 2009, Fancy and Bennetts 2012).

In this study, we move beyond bioassessment and use NPS I&M wetland monitoring data to address questions about how degradation in ecological integrity relates to specific human activities. Building from a set of wetland attributes previously identified as sensitive bioindicators of HD in RMNP, we use structural equation modeling (SEM; Grace 2006) to evaluate hypotheses about how specific human activities might influence bioindicators. We first present a general hypothesis for how human activities may affect wetland integrity and then develop a specific model that can serve as a basis for natural resource management strategies, critical to meeting the mission of the NPS for RMNP wetlands (Bennetts et al. 2007, U.S. NPS 2007).

Study system and background

We conducted our work in RMNP (Fig. 1). Established by Congress in 1915, RMNP encompasses 1075 km^2 in north-central Colorado, United States. The park preserves the high-elevation ecosystems and wilderness character of the southern Rocky Mountains and provides recreational use of and access to the park's scenic landscapes, wildlife, natural features and processes, and cultural objects. Schweiger et al. (2015) estimated that in 2007, there were approximately 4100 ha of wetland covering around 4% of the park's area. Most park wetlands are of three types (Cooper et al. 2012, Gage and Cooper 2013): Approximately 21% are fens (organic soils and groundwater-driven stable and high water tables), ~37% are wet meadows (mostly mineral soils, variable hydrology), and ~39% are riparian (mineral soils, surface water-driven, seasonally high water tables).

Wetlands in RMNP support a surprising proportion of the park's biodiversity. For example, we recorded 465 vascular and 73 nonvascular plant taxa in our 154 wetland sites—more than 30% of the park's total known flora (E. Schweiger, *unpublished data*). Approximately 65% of the rare

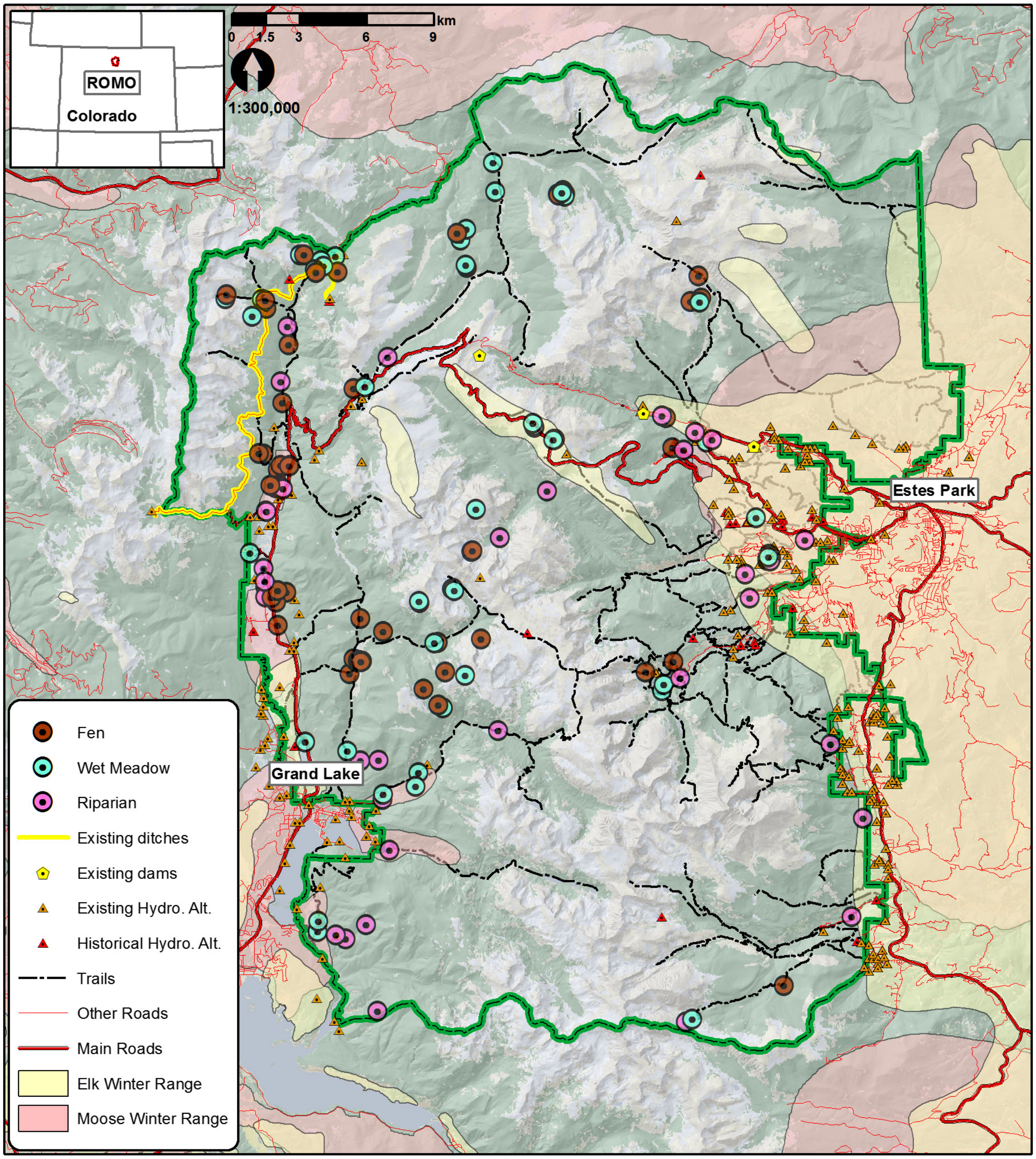

Fig. 1. Rocky Mountain National Park, Colorado, United States. Map shows park boundaries and all 154 sites used in the structural equation model by wetland type. Prominent existing and historical human disturbance features (roads, ditches, diversions, drainage tiles, and dams) are mapped using point and linear symbols. Elk and moose winter ranges are shown with pink and yellow shading. Gateway communities of Grand Lake and Estes Park are shown on the west and east sides of the park. Inset gives location of the park in Colorado.

or imperiled plant communities in RMNP are in wetlands (RMNP 2004). In addition, 45% of the park's avian species and 20% of its mammals use wetlands for key phases of their life history (M. Britten, *unpublished data*). Finally, wetlands are core habitat for elk and beaver, two of the park's iconic native species. These wetland biodiversity functions link to pressing resource management challenges for the park: (1) maintaining biodiversity and (2) preserving and restoring the habitat that supports charismatic fauna (Britten et al. 2007, U.S. NPS 2007).

Humans have directly and indirectly affected RMNP wetlands since before the park was established. Direct human alterations of hydrologic processes in RMNP include small-scale features such as water supply reservoirs and drainage ditches and, more significantly, large-scale diversions that influence around 44% of the park's area (Figs. 1, 2; E. Schweiger, *unpublished manuscript*). The largest in the park (still operational) is the 20 km long Grand Ditch that diverts up to 40% of the Colorado River's annual runoff each year (Chimner and Cooper 2003, Woods and Cooper 2005), significantly impacting the hydrologic regimes of many wetlands. Other disturbances have directly removed or degraded wetland vegetation, soils, and buffer areas. For example, the park historically contained several commercial operations including a golf course and ski area (Fig. 2) that caused local disturbances (i.e., cutting ski runs) and also larger-scale effects from supporting facilities. During the late 1800s and early 1900s, the park and private landowners planted Eurasian pasture grass species, especially in wetlands, to support trail stock and ranching operations.

Historical disturbances can have persistent impacts that interact with and add to the effects of current park operations and visitor support services. The park has always had high visitation, with approximately 3 million visitors each year since 1970 (U.S. NPS 2015) and more than 4 million in 2015, ranking RMNP third in visitation within the NPS. Within the 1075-km^2 park, there are approximately 170 km of roads (40 km paved), 327 culverts for stream and other crossings, 536 km of trails, 107 backcountry campgrounds, five major front country campgrounds, and three visitor centers, all with groundwater withdrawals for drinking water and sanitation services. In addition, there are 33 modest private inholdings and housing for park staff inside the park's boundaries.

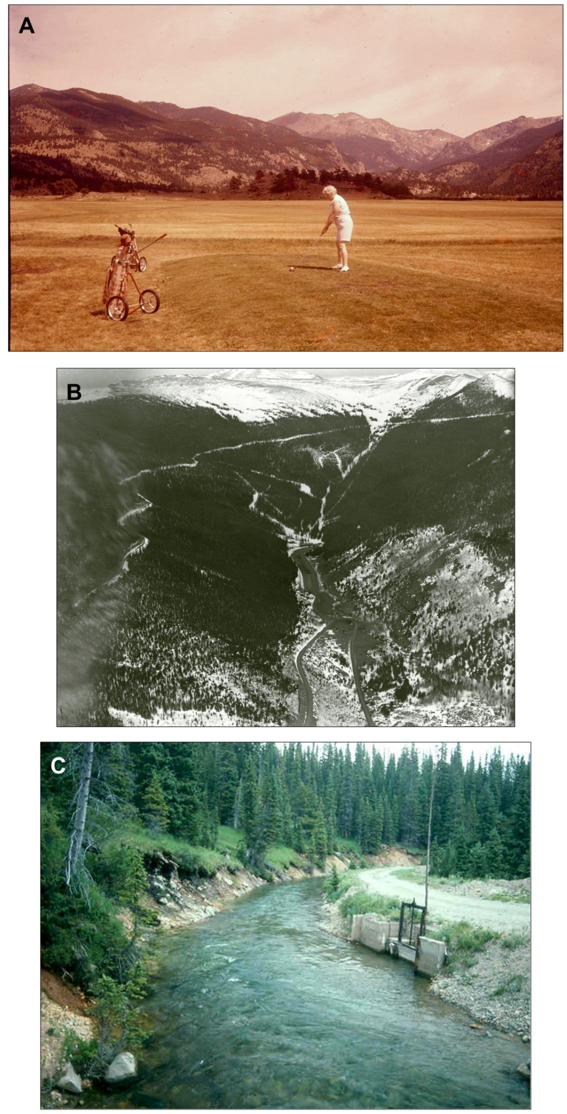

Fig. 2. Examples of historic and current small- and large-scale human disturbances in Rocky Mountain National Park (RMNP): (A) Moraine Park golf course, circa 1955; (B) Hidden Valley ski area in 1973 showing ski runs, parking areas, an associated blowdown, and Trail Ridge Road; (C) the Grand Ditch with its supporting road and a headset in 2014. Images in A and B courtesy of RMNP. Image in C by D. Cooper.

National Park Service resource management, including in RMNP, shifted toward natural resource conservation in the late 1970s (Sellars

1997). RMNP removed all water storage reservoirs by 1980 and most intensive commercial visitor facilities by 1990. Overall, a comprehensive path toward ecosystem restoration was well in place within park resource management by the mid-2000s. Nevertheless, residual impacts from historical modification, ongoing visitor support, and general park operations continue to impact wetlands (Cooper et al. 2006, Tousignant et al. 2010, Kaczynski and Cooper 2015*b*).

Some of the more complex impacts from historical and ongoing human land use in RMNP are on apex predators that drive ecological processes central to the park's wetlands. The influence of large predators on wetlands is complex (i.e., Marshall et al. 2014); however, trophic downgrading (Estes et al. 2011) from predator removal has likely contributed to degraded wetland condition in RMNP. Human activities extirpated (*Canis lupus*) wolves largely before the park was established, and (*Ursus horribilis*) grizzly bear disappeared soon after (Armstrong 1987). The park actively controlled other predators from 1917 to 1926 to encourage recovery of ungulate populations (Stevens 1980). Wolves may have a significant effect on elk populations (Jenkins and Wright 1987, Fortin et al. 2005). The ability of grizzlies to control elk populations may be largely compensatory (Cole 1972), although they can play an important role via predation on calves (Middleton et al. 2013). Existing black bear (*Ursus americanus*) and mountain lion (*Puma concolor*) populations in RMNP are not effective controls of large ungulates. The return of wolves and grizzlies to the park and the surrounding area has not occurred for a variety of ecological and social reasons (U.S. NPS 2007). Through 2015, RMNP had no plans to restore gray wolves (Marshall et al. 2014) but will manage the system with state and other federal partners accordingly should they return on their own. Grizzly bears are not likely to naturally recolonize the park and there are no plans to reintroduce them to the area.

There have been important direct and indirect consequences from historical and ongoing anthropogenic disturbances on the abundance and distribution of large ungulates and beaver (*Castor canadensis*) and on the interactions among these species and their wetland habitat. Trapping nearly extirpated beaver by the 1940s (Packard 1947). Populations marginally recovered by the 1980s (Stevens and Christianson 1980). However, by the mid-1990s, they were outcompeted by elk (*Cervus elaphus*) and more recently, nonnative moose (*Alces alces shirasi*), such that by 2015 there were likely only a few beaver resident in the park. Consistent estimates of elk annual total population size for the park as a whole are not available. However, it is clear that elk numbers have varied spatially and temporally, driven by anthropogenic factors and natural controls (Singer et al. 2002, Zeigenfuss et al. 2002). Ketz et al. (*in press*) provided rigorous results for a subset of the park (winter range on the east side) that show numbers varied from around 500 in 1970 to 1500 in 2001 to 300 in 2015. Peak elk numbers in the early 2000s were at or above the carrying capacity of the winter range as independently estimated by Hobbs et al. (1982) and Lubow et al. (2002). Moose were introduced to Colorado in 1978 (Bergman et al. 2013, CPW 2013), and these large wetland dependent herbivores were first observed in the park in the summer of 1980 (U.S. NPS 2007, Dungan et al. 2010). Moose numbers and range continued to increase through 2015 (J. Dungan, *personal communication*). While it is not clear whether the effect of elk or moose on beaver and wetland condition is density dependent, research has shown that even at lower numbers, elk and moose do degrade wetlands and can outcompete beaver (Singer et al. 2002, Baker et al. 2012).

Ecosystem engineering by beaver has been a key driver of hydrologic regimes in many RMNP wetlands (Westbrook et al. 2006, 2011). Yet beaver have not been a functional part of the park's wetlands since the mid-1990s (Singer et al. 1998, 2002, Baker et al. 2012) when elk exceeded their carrying capacity (Hobbs et al. 1982, Coughenour 2002, Lubow et al. 2002) and moose began to increase. The functional loss of beavers creates a detrimental positive feedback with fewer beaver dams resulting in altered hydrologic regimes that no longer support recruitment of willows and other woody species that beavers use for forage and dam building materials. An analysis of the potential role of wolf predation on elk dynamics, beaver, and wetland vegetation in RMNP indicated that wolves could effectively control elk numbers and distribution with subsequent positive effects on vegetation cover, indicating important top-down control (sensu Estes et al. 2011) and the consequences of human predator removal (Coughenour 2002). Yet, willow cover only recovered completely in a model that included the restoration of hydrologic regimes and beaver. RMNP resource management considers the reference state for the wetlands in the park to include sustainable populations of beaver and large ungulates supported by intact stands of willow and aspen with hydrologic regimes that maintain native wetland vegetation communities and all wetland functions (U.S. NPS 2007).

Ecologists have studied large ungulate and beaver interactions in RMNP and across the American West (i.e., Coughenour 2002, Zeigenfuss et al. 2002). Current management in RMNP is based on these scientific findings (U.S. NPS 2007; Ketz et al., *in press*). However, most previous work in RMNP and elsewhere has not integrated the effects of historical or current HDs and important environmental gradients with the role of ungulates and their predators in influencing wetland condition. Moreover, research to date in the park has limited indicators of wetland condition to herbaceous understory diversity, which can be difficult to interpret (Chew 1982, Gough and Grace 1998), or woody vegetation composition and structure, which may not reflect contemporary wetland integrity. Perhaps most importantly, previous analyses of ungulates, beavers, and wetlands in RMNP have not quantitatively examined the network of connections that allows a more complete description of the drivers controlling ecosystem condition (Kaczynski and Cooper 2013). The demonstrated influence of multiple drivers on wetland condition argues that such an analysis will inform important changes in wetlands management strategies in the park.

Wetland condition in Rocky Mountain National Park

We present an overview of the bioassessment of wetland condition in RMNP in Appendix S1. We summarize this work here. First, we developed a HD index (also used in the SEM), to estimate important direct and indirect anthropogenic disturbances affecting wetlands. We derived HD from a compilation of extant disturbances and the residual effects of historical human use as introduced above. We then used methods modified from Stoddard et al. (2008) to create a multimetric index (MMI) based on HD and a large set of candidate biometrics (see also Karr 1991, DeKeyser et al. 2003, Rocchio 2007*a*, Deimeke et al. 2013, Schoolmaster et al. 2013*a*, *b*, Wilson et al. 2013). We also developed park-specific thresholds in the distribution of MMI scores from regression tree models to delineate boundaries between reference and nonreference wetland condition states (e.g., Stoddard et al. 2006). Using these thresholds and design-based statistical inference (allowed by the survey design, Olsen et al. 1999, Stevens and Olsen 2004), we estimated that approximately 31% of fens, 49% of wet meadows, and 42% of riparian wetlands were in a human-disturbed, or nonreference, condition in 2007–2009. Fig. 3 provides visual examples of high- and low-integrity wetlands in the park based on MMI and HD scores. High-integrity riparian sites (Fig. 3A: MMI score 9.9 on a scale of 1–10, with 10 being high integrity; HD score 5.5 on a scale of 1–100, with 100 being high disturbance) are characterized by a low degree of invasion, high cover of species with strong wetland affinity, high conservatism, and high cover of native forbs (herbaceous dicot life-form). The site in Fig. 3A is within one of the few active beaver complexes in the park. Low-integrity wet meadow sites (as in Fig. 3B: MMI score 2.2; HD score 73.6) are characterized by a high degree of invasion, low diversity of native species—especially those with high wetland affinity, low conservatism, and low cover of woody taxa. In general, most disturbed wetlands are in large valley bottoms where historical human land use was concentrated. This is also where most current visitor use and facilities occur, where core elk and moose winter range overlap, and where most beaver once lived in the park.

In the process of constructing MMIs, we observed that three key wetland community attributes were consistently sensitive to HD and might serve as interpretable biometrics of ecosystem integrity: conservatism, degree of invasion, and native forb cover (especially in riparian and wet meadow communities). Of these three, conservatism and degree of invasion are well known and useful indicators for many, if not most, types of plant communities. Native forb cover is perhaps more novel or potentially specific to wetlands in RMNP. Collectively, these three aspects of wetland vegetation have strong management application, are relatively easy to measure, are ecologically distinct and independent, and often

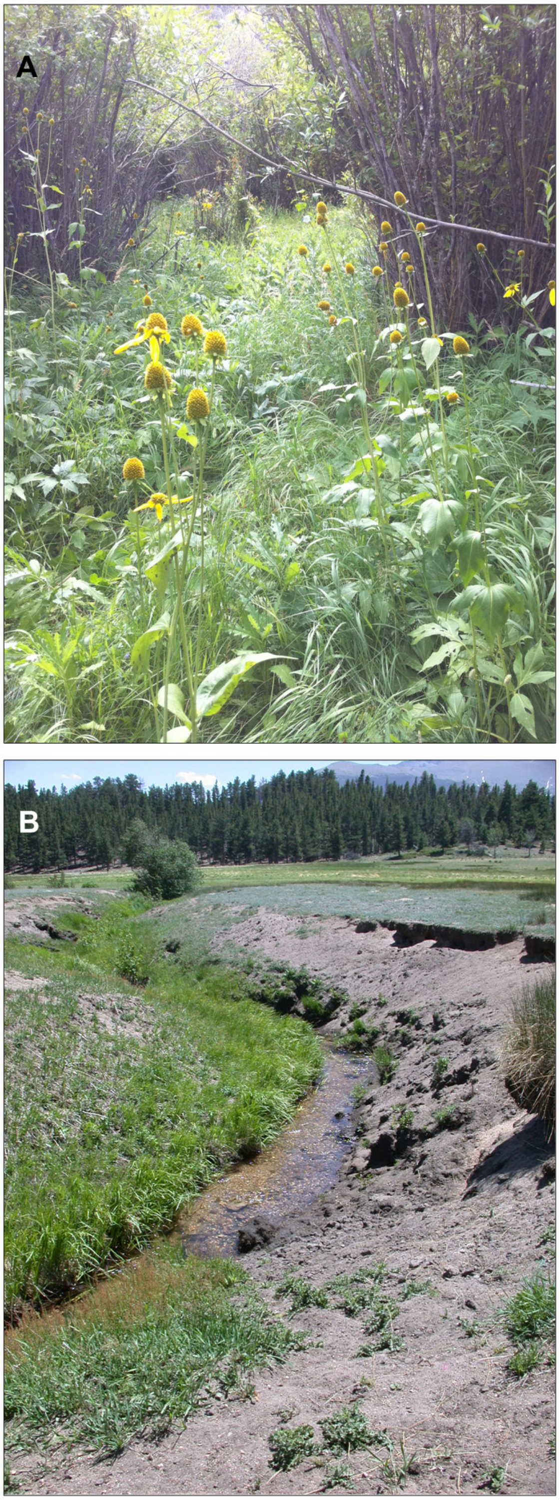

Fig. 3. Representative examples of sites with (A) high and (B) low wetland ecological integrity based on a bioassessment of the wetlands in Rocky Mountain National Park. See main narrative and Appendix S1 for more details. Images by E. W. Schweiger.

appear in studies of wetland condition (Ervin et al. 2006, Johnston et al. 2008).

The conservatism of a species is defined as its degree of fidelity to a specific habitat or range of environmental conditions (Wilhelm and Ladd 1988, Herman et al. 1997, Matthews et al. 2015). Anthropogenic impacts usually cause dramatic shifts in ecological processes and habitat conditions and push disturbance regimes outside a natural range of intensity, frequency, and duration. Species that are more conservative are not able to adapt to human-induced alterations compared with broad-niche generalists and are often the first to disappear from habitats impacted by human activities. We use an expert-derived metric of the degree of conservatism in a wetland community calculated as the mean of conservatism scores (also known as "C-scores," Rocchio 2007*a*, *b*) for all species in a sample. Species with high C-scores are obligate to high-quality natural areas and cannot tolerate habitat degradation.

Invasive species have well-established undesirable effects on ecosystem function (Byers et al. 2002, Levine et al. 2003, Fridley et al. 2007). Invasive species have been linked to reduced overall species diversity (Meiners et al. 2001), altered resource dynamics (Ehrenfeld 2003), and shifted interactions between species (Christian and Wilson 1999). We calculate a community-scale degree of invasion following Iacona et al. (2014) by averaging the relative cover-weighted scores of the invasiveness of all species in a sample (also known as "I-ranks," Morse et al. 2004). Species with high I-ranks tend to alter ecosystem processes, have wide geographic distribution, are difficult to control, and can cause substantial impacts to rare or vulnerable species.

Native forb cover has two aspects—native vs. nonnative and forbs vs. nonforbs. Nativity is often positively correlated with integrity (i.e., Botkin 2001, Ervin et al. 2006), and maintaining

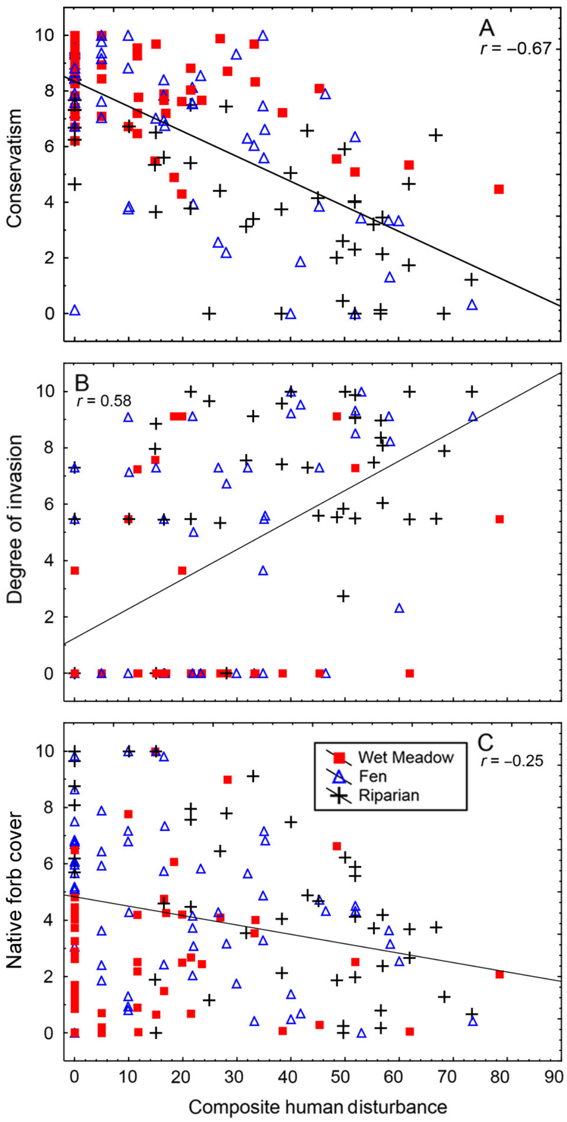

Fig. 4. Bivariate relationships between composite human disturbance (HD) and biometrics showing with increasing levels of HD: (A) decreasing conservatism, (B) increasing invasion, and (C) marginally decreasing native forb cover. All response data are transformed following Blocksom (2003). Pearson's correlation coefficient (r) reported in each panel. Solid red squares identify wet meadow sites, hollow blue triangles identify fen sites, and black crosses identify riparian sites.

native or eliminating nonnative species are typical goals of most resource management agencies, including the NPS (U.S. NPS 2006). The differential response of forbs is less obvious, but appears quite important for RMNP wetlands. We estimate this metric as the absolute cover of native forbs in a sample, with nativity and life-form as determined by Weber and Wittmann (2001).

For the current study, we used these three wetland community attributes to serve as indicators of ecological integrity (Karr and Chu 1999). We analyzed relationships involving individual biometrics rather than a MMI of integrity (see Appendix S1; note that data are the same in the two sets of analyses). We interpret the relationship between the biometrics and the broader concept of integrity such that higher conservatism, lower degree of invasion, and, in most cases, higher native forb cover are associated with greater degrees of ecological integrity. The net relationships between the three bioindicators and HD (Fig. 4) indicate that with increasing HD, wetlands tend to possess lower conservatism and a higher degree of invasion. The relationship between HD and native forb cover tends to be negative with the pattern most clearly seen in riparian wetlands.

A general hypothesis for how human activities affect wetland integrity

We present our general hypothesis as a metamodel (sensu Grace et al. 2010) identifying key dependencies that may drive wetland condition responses to human activities (Fig. 5). We base the metamodel on the literature and our combined experience in wetland ecology generally and in RMNP specifically. Our metamodel includes both variables and relationships that are contemporary (solid lines and boxes) or relictual (dashed lines and boxes). The metamodel is used to guide the specification and interpretation of the structural equation (SE) model presented in the *Results* section.

Beaver strongly influence the dynamics of RMNP wetlands (link 1 in Fig. 5). This may happen even in their absence because remnant dams, channels, and landforms created when beaver were present continue to alter surface water distribution and hydrodynamics, leading to elevated groundwater levels. In wetlands that support beaver and ungulates, shrub productivity is critical (link 2). High shrub production generally leads to elevated levels of standing shrub biomass (link 3), which in turn may attract ungulates (link 4). More ungulates create higher

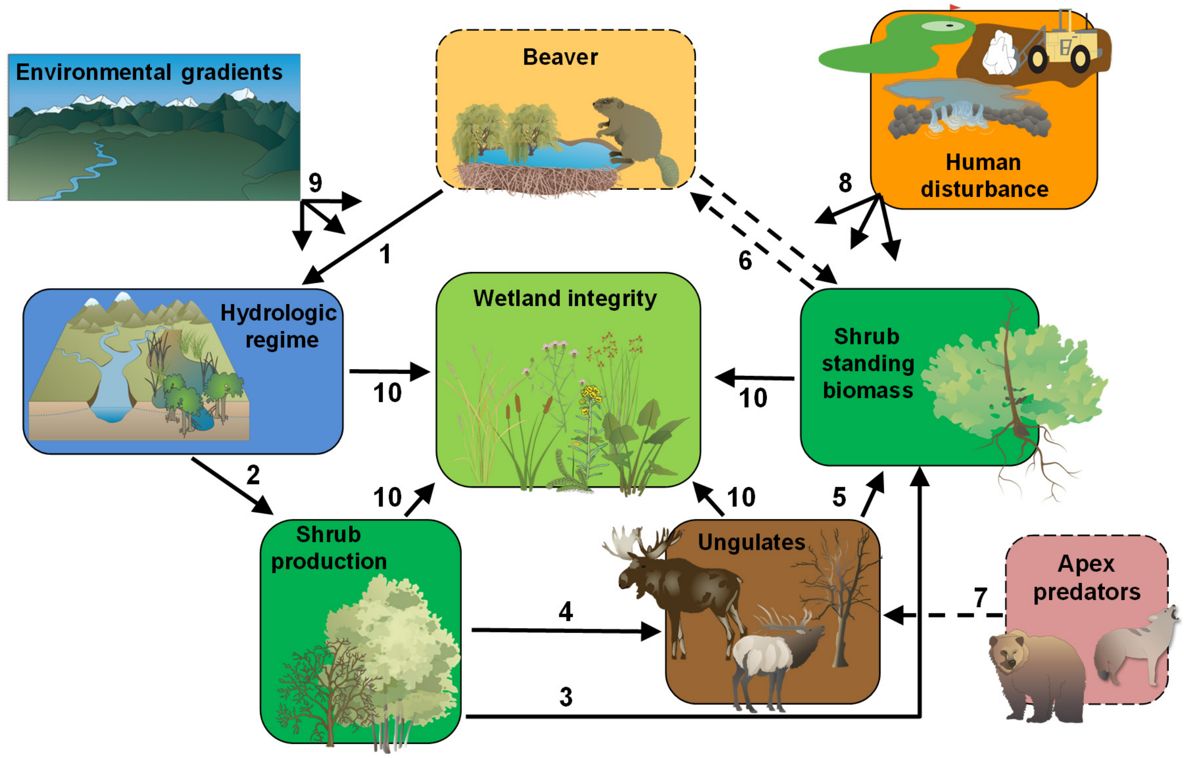

Fig. 5. Metamodel representing a general hypothesis of the key interrelationships driving wetland integrity responses to human activities. Dotted arrows and borders indicate historical relationships or model elements no longer functionally present, but included in the model to capture important historical patterns and demonstrate possible restoration avenues. Graphics in each box illustrate each concept. Graphics are courtesy of Integration and Application Network, University of Maryland Center for Environmental Science.

levels of browsing and shrub biomass removal (link 5). Shrub biomass is important in wetlands (especially riparian systems) in numerous ways. Shrubs are critical food and building material for beaver, and in areas with beaver populations, tall shrub biomass is a limiting resource (link 6—completing the primary loop within the model). Factors that influence this cycle include apex predators (or the lack thereof; link 7), HD (link 8), and a suite of environmental gradients (link 9). Human disturbance can directly and indirectly alter most elements in the metamodel—beaver, hydrologic regime, apex predators, climate, etc. (at least some geophysical gradients like elevation are immune from our reach).

Interactions between direct and indirect HD, hydrologic regime, shrubs, and ungulates are of key interest in this study. While beaver are nearly functionally absent from the park and wolves and grizzlies were extirpated long ago, we still include them in the metamodel to indicate their once important roles and because they represent important potential pathways to ecosystem restoration and maintenance of wetland integrity. Finally, wetland integrity biometrics respond directly to hydrologic regime, shrub production, ungulate habitat use, and shrub biomass (link 10) and indirectly to beaver, apex predators, environmental gradients, and HDs.

Methods

Data collection

Schweiger et al. (2015), Appendix S2, and Table 1 present field methods and summaries of the metrics used in the SE model. Data were collected at 154 wetlands (see Fig. 1) selected using two sample designs. First, a parkwide spatially balanced probability survey (Stevens and Olsen 2004, Schweiger et al. 2015) located 96 "survey"

Table 1. Field measures and computed variables used in RMNP SE model.

Variables	Source	Details	Mean	Range	SD	SE
Native forb cover (%)	Field data	Average cover of native forbs	18.3	0 to 76.3	14.21	1.15
Hydric conditions (index)	Derived from field data	Cover-weighted wetland affinity score: Higher values describe communities characterized by more obligate wetland plants (Tiner 2012)	4.3	2.5 to 5.0	0.6	0.05
Degree of invasion (index)	Derived from field data	Cover-weighted degree of invasion: Higher values are more invaded communities (Morse et al. 2004)	2.0	0 to 7.0	2.22	0.18
Conservatism (index)	Derived from field data	Mean conservatism score: Higher values are more conservative communities (Rocchio 2007*a*, *b*)	6.3	3.6 to 7.8	0.9	0.07
Composite HD (index)	Derived from field and GIS data	Higher score is higher composite HD	22.4	0 to 78.6	21.53	1.73
Hydrologic alteration (index)	Field data	Higher score is more human-altered hydrologic regimes	2.9	20,12,4,0	5.04	0.41
Natural land use/cover in buffer (%)	Derived from field data	Higher percentage is more natural land use or cover types within sites of 100-m buffer	90.4	0 to 100	13.55	1.09
Road buffer (m)	GIS measure	Linear distance to nearest road of any type	1765.2	0 to 8103	2181.54	175.79
Soil disturbance (index)	Field data	Higher score is more human-altered soil	1.0	10,7,3,0	2.2	0.18
Shrub tall Production (index)	Derived from field data	Production of >2-m tall shrubs	7.4	0 to 93.5	16.35	1.32
Shrub short production (index)	Derived from field data	Production of <2-m tall shrubs	2.9	0 to 21.3	4.65	0.37
Shrub all production (index)	Derived from field data	Production of all shrubs	10.3	0 to 96.0	18.48	1.49
Ungulate activity (index)	Field and GIS data	Higher score is greater ungulate habitat use	4.8	10,7,3,0	3.94	0.32
Shrub all browsed (index)	Derived from field data	Ungulate browse on all shrubs	18.0	0 to 154.0	24.93	2.01
Shrub tall browsed (index)	Derived from field data	Ungulate browse on >2-m tall shrubs	6.1	0 to 82.5	13.55	1.09
Shrub all biomass (index)	Derived from field data	Living biomass of all shrubs	6.3	0 to 84.6	13.16	1.06
Shrub tall biomass (index)	Derived from field data	Living biomass of >2-m shrubs	4.3	0 to 82.3	11.68	0.94
Groundwater level (cm)	Field data	Late summer depth to groundwater from soil surface	−28.8	−125.0 to 7.4	29.21	2.35
Historical beaver activity (index)	Field and GIS data	Higher score indicates greater historical beaver remnant habitat features	0.6	10,7,3,1	1.89	0.15
Distance core elk habitat (m)	GIS	Linear distance to nearest core elk habitat (CPW 2014)	1233.2	0 to 5503	1394.67	112.39
Elevation (m)	GIS	Elevation above sea level	2960.6	2377 to 3820	338.95	27.31
Meadow (categorical)	Field data	Groundwater-fed mineral soil wetland type		1,0		
Organic soil (%)	Field data	Percentage organic carbon at 40 cm	22.8	0.6 to 87.8	26.67	2.15
Topographic dryness (index)	GIS	Low values indicate landscapes that gather more water, while high values are convex areas with more runoff	239,120	150,514 to 438,644	70,445.19	5676.64
Riparian (categorical)	Field data	Wetland type influenced by the hydrologic and geomorphic processes of streams		1,0		
Slope (degrees)	GIS	Mean slope in sites catchment	19.3	4.5 to 34.7	5.78	0.47
Precipitation (cm)	30-yr normals (PRISM 2014)	Total precipitation in sites catchment	88,871.5	44,938 to 117,887	17,186.73	1384.95

Notes: HD, human disturbance; RMNP, Rocky Mountain National Park; SE, structural equation.
See Appendix S2, Data S1, and Schweiger et al. (2015) for more details.

sites across the park. The randomized approach used to select survey sites ensures that sampled wetlands were representative of all wetlands in the park and that broad gradients in elevation, slope, wetland context, disturbance regimes, soils, hydrologic regimes, and vegetation type were included. Second, we used a targeted design to locate 58 "sentinel" sites in wetlands with a specific known or expected ecological context. Sites were targeted to wetland complexes with either heavily disturbed or near pristine hydrologic regimes, soils, and vegetation. Disturbances impacting these wetlands included anthropogenic features and land use (such as roads and trails), historical and/or ongoing hydrologic modification, and "natural" drivers such as ungulate habitat use and beaver habitat modification (or the lack thereof where it was expected). Sentinel sites ensured that complete gradients of disturbance and site contexts were included in our data set. We used a classification of wetland into fens, wet meadows, and riparian wetland (Cooper et al. 2012, Gage and Cooper 2013) to help structure both designs and ensure roughly similar sample sizes for each wetland type. Importantly, given the use of both a probabilistic and targeted design, we make no statistical inference beyond the sites included in our SE model. We determined that it was more important to include a larger sample size that captured more of the wetland condition gradient in the park than to infer SE results using design-based methods to unsampled wetland.

We collected data from each site from one to six times in 2007 and 2008 (with fewer samples in 2009–2011) as close to peak summer vegetation development as possible (mid-July through mid-September, depending on the year and site). Vegetation composition, soil structure/chemistry, water table depth, and disturbance regimes were all relatively similar from 2007 to 2011 (Schweiger et al. 2015). We chose events with vegetation closest to peak phenological development for sites with more than one sample over these years. Over 160 additional sample events taken during these years were not included in the SE model. We used these data to calibrate and adjust field methods, to estimate the quality of metrics and for various other quality assurance purposes (Schweiger et al. 2015). Of note, all data and metrics used here meet or exceed quality assurance and control requirements as defined in Britten et al. (2007) and U.S. EPA (2011).

Structural equation modeling

We used SEM for this application to evaluate hypotheses about how human activities may connect to wetland integrity metrics (Grace 2006). We chose SEM instead of traditional statistical modeling because it allows for the specification of system-level network hypotheses. To clarify, traditional statistical models are of the form $y = f(\mathbf{X})$, where y is some response variable of interest and $\mathbf{X}$ is a vector of predictor variables. However, this equational form provides no means for representing hypotheses about why x variables might be correlated. In contrast, SE models are of the form $\mathbf{Y} = f(\mathbf{X}, \mathbf{Y})$, which allows for the specification of network hypotheses in which each variable is seen to be part of a system of variables. As a result, we may test the idea that variable C is influenced by variable A through the mediating effect of B (i.e., $A \rightarrow B \rightarrow C$). This flexibility in equational representation has numerous benefits, including the representation of more complete hypotheses and the discovery of unanticipated relationships (e.g., effects of A on C not through B).

Our investigation was "mediation focused" (Grace et al. 2012) in that we wished to determine the various indirect pathways whereby human activities ultimately can lead to changes in integrity. We began with the prior observation that certain attributes of the wetland plant communities are related to gradients in HD (see Fig. 4). We then evaluated hypotheses about how these net associations are mediated. Our knowledge of the system (see our general hypothesis and Fig. 5) provided us with a framework (Grace et al. 2010) for building a SE model that represents a series of specific hypotheses supported by available data. All analyses were carried out in R version 3.2.3 (R Development Team 2014) with select graphics produced in Statistica version 12 (StatSoft 2013) or Visio (Microsoft Office Visio Professional 2003). All *R* scripts and data are included in the Supporting Information for this study.

Transitioning from a metamodel to a SE involves consideration of how theoretical constructs, such as HD or shrub production, are to be represented as measurable quantities. For all theoretical constructs in our metamodel, we considered a set of possible measurements for external validity (an expert's view of how these generalize across similar systems) and statistical reliability. Model construction proceeded in piecewise fashion, initially relying on the evaluation of single-node submodels, followed by a global assessment of model-data consistency (Grace et al. 2015). Measured variables ultimately selected for inclusion in the final model are summarized in Table 1.

Most details of the SE model developed in this study are presented in our *R* script. We used a variety of model specifications, depending on the nature of the responses. Variables were log-transformed as necessary to maximize linearity of relationships. We modeled tall and short shrubs separately because beaver are dependent on tall shrubs, while ungulates can use both tall and short shrubs. We modeled tall shrub production using a strategy designed to address zero inflation from multiple causes. First, we developed a filter based on the upper elevational limit for tall shrubs (3400 m). Second, we modeled the presence or absence of tall shrubs as a binomial response. Third, we modeled positive productivity values using a linear, normal specification. We then combined the probability estimates from these steps into a single prediction equation using the method of Fletcher et al. (2005). Short shrub production was modeled in a similar fashion, although without an upper elevation limit. We computed the production of all shrubs directly from the combination of tall and short shrub production estimates. We modeled ungulate activity, which was scored by field crews on a 10-point scale, using a proportional odds approach (Agresti 2010). We modeled all other endogenous variables (a variable in the model that is influenced by other variables in the model, i.e., a dependent variable; Grace 2006) as normal responses. We considered nonlinear relations between predictors and responses in all cases, but did not find such elaborations to improve model fit.

For this application, whose objective was interpretation rather than prediction only, we based variable and model selection on multimodel comparisons using sample size-corrected Akaike Information Criterion (AICc) values, with the additional requirement that relationships included were mechanistically interpretable (to avoid spurious overfitting; Cade 2015, Fieberg and Johnson 2015). In all cases, models selected using local estimation were either the best model based on AICc or equivalent to the best model (within two units of the best model). Final models were checked by examining residual relationships for indications of omitted linkages (Grace et al. 2012). Finally, predicted–observed plots were also examined to understand any limits to extrapolability.

We report both raw and standardized coefficients. Because of the complexity of some linkage functions, we developed standardized coefficients based on relevant ranges (Grace and Bollen 2005) rather than standard deviations using a query-based approach (Grace et al. 2012). Standardized coefficients are interpreted as the predicted change in a variable along its range in response to varying a predictor along its range of values. The total coefficient for a pathway (or a series of connections) between a predictor and a response is derived as the product of all coefficients in the pathway. Total coefficients can be small because they accumulate error through each link. However, when considering indirect effects, it is important to realize that interventions along the chain can have quite large effects, particularly when conducted within a subset of the entire sample of wetlands (Grace et al. 2012).

Results

Structural equation model-data fit was found to be adequate and no missing linkages could be detected (Fig. 6). Table 2 gives the submodels for each response, the model-adjusted r^2, and for each predictor, raw and standardized coefficients with the standard errors for raw coefficients.

Effects on conservatism

Fig. 7 isolates the predictors and pathways leading to conservatism (compare with Fig. 6). There are five direct predictors in the final submodel, accounting for 64% of the variation in conservatism in our data set. Decreasing composite HD and higher elevations directly and strongly predict higher levels of conservatism. Conservatism is also higher under more hydric conditions. There are negative effects of riparian and wet meadow wetland type (relative to fen), suggesting that fens support the most conservative species assemblages.

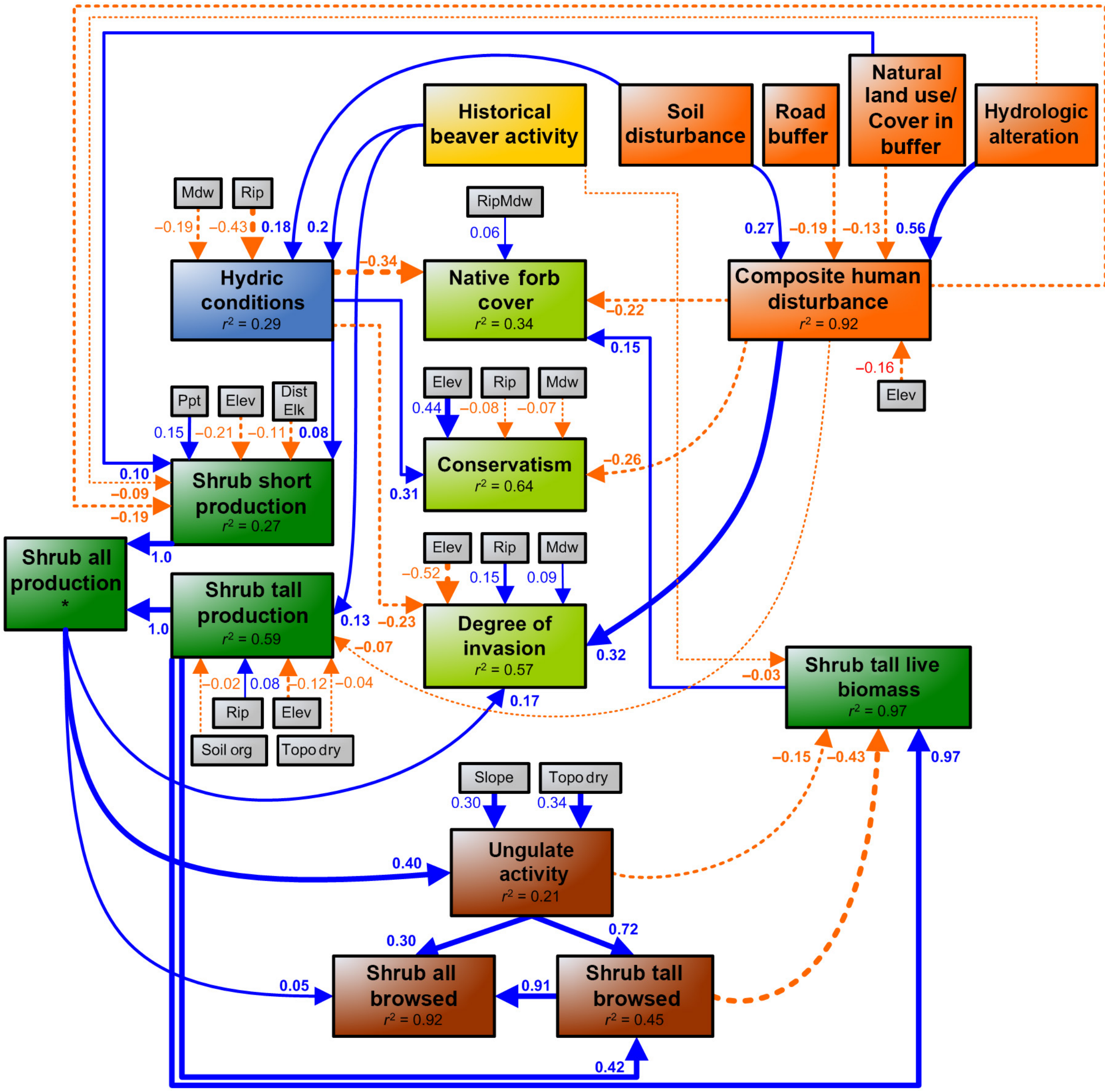

Fig. 6. Complete structural equation model showing primary connections discovered and variance explanation for each node. Blue coefficients and solid lines indicate positive relationships. Orange coefficients and dotted lines indicate negative relationships. Line width varies with the standardized coefficient value. Node color is grouped by the general type of response: orange for human disturbance, yellow for beavers, blue for hydrology, dark green for shrubs, brown for ungulates, gray for environmental gradients, and light green for biometrics. Additional details are presented in Table 2. The shrub all production submodel is a simple calculation from shrub short and shrub tall production and has no r^2.

There are a total of six indirect pathways linking predictors to conservatism. All four components of composite HD have indirect effects on conservatism acting through HD: Hydrologic alteration strongly reduces conservatism; increasing anthropogenic soil disturbance reduces conservatism; conservatism is higher further from roads; and more natural buffer area increases conservation. The fifth indirect effect observed is a pathway from human soil disturbance

Table 2. Summary of all submodels, predictors, raw coefficients, standard errors, and adjusted r^2.

Submodel/predictors	Raw coefficient	SE	Range standardized coefficient
Composite HD; adjusted $r^2 = 0.92$			
Intercept	68.802	7.630	–
Hydrologic alteration	0.441	0.024	0.562
Road buffer	−2.309	0.407	−0.187
Natural land use/cover in buffer	−0.192	0.051	−0.133
Soil disturbance	2.136	0.259	0.272
Elevation	−0.009	0.002	−0.160
Hydric conditions; adjusted $r^2 = 0.29$			
Intercept	4.627	0.068	–
Soil disturbance	0.045	0.018	0.183
Riparian	−1.066	0.108	−0.434
Meadow	−0.466	0.092	−0.189
Historical beaver activity	0.052	0.023	0.210
Shrub tall production; adjusted $r^2 = 0.59$			
Intercept	6.881	3.202	–
Composite HD	−0.027	0.013	−0.069
Riparian	1.756	0.482	0.076
Elevation	−0.003	0.001	−0.121
Historical beaver activity	0.384	0.186	0.131
Intercept	4.571	0.593	–
Topographic dryness	0.000	0.000	−0.044
Organic soil	−0.012	0.007	−0.024
Shrub short production; adjusted $r^2 = 0.27$			
Intercept	4.974	2.564	–
Hydrologic alteration	0.020	0.014	0.086
Composite HD	−0.043	0.020	−0.191
Hydric conditions	0.547	0.305	0.082
Distance core elk habitat	0.000	0.000	−0.113
Elevation	−0.003	0.001	−0.212
Precipitation	0.000	0.000	0.146
Intercept	0.198	0.553	–
Natural land use/cover in buffer	0.012	0.006	0.101
Shrub all production†			
Shrub all production	–	1.000	–
Shrub all browsed; adjusted $r^2 = 0.92$			
Intercept	−0.076	0.128	–
Shrub all production	0.015	0.006	0.053
Shrub tall browsed	0.997	0.035	0.912
Ungulate activity	0.079	0.022	0.300
Shrub tall browsed; adjusted $r^2 = 0.45$			
Intercept	−0.471	0.289	–
Shrub tall production	0.108	0.011	0.420
Ungulate activity	0.174	0.048	0.723
Ungulate activity; adjusted $r^2 = 0.21$			
Intercept	−3.807	0.375	–
Shrub all production	0.586	0.043	0.400
Topographic dryness	0.000	0.000	0.340
Slope in catchment	0.060	0.011	0.300
Shrub tall biomass; adjusted $r^2 = 0.97$			
Intercept	0.410	0.270	–
Shrub tall production	0.853	0.014	0.970
Shrub tall browsed	−1.456	0.076	−0.427
Historical beaver activity	−0.212	0.094	−0.026
Ungulate activity	−0.123	0.047	−0.149

Table 2. Continued.

Submodel/predictors	Raw coefficient	SE	Range standardized coefficient
Conservatism; adjusted $r^2 = 0.64$			
Intercept	2.264	0.661	–
Composite HD	−0.013	0.003	−0.255
Elevation	0.001	0.000	0.435
Riparian	−0.346	0.149	−0.082
Meadow	−0.288	0.112	−0.068
Hydric conditions	0.141	0.089	0.082
Degree of invasion; adjusted $r^2 = 0.57$			
Intercept	10.884	1.850	–
Composite HD	0.029	0.007	0.323
Elevation	−0.002	0.000	−0.516
Riparian	1.074	0.416	0.154
Meadow	0.648	0.312	0.093
Hydric conditions	−0.641	0.248	−0.226
Shrub all production			
Native forb cover; adjusted $r^2 = 0.34$			
Intercept	67.962	7.398	–
Composite HD	−0.210	0.045	−0.216
Hydric conditions	−10.487	1.774	−0.338
Shrub tall biomass	0.136	0.081	0.147
Riparian and meadow	4.171	2.329	0.055

Notes: HD, human disturbance. See Appendix S2, Data S1, and Schweiger et al. (2015) for more details. Standard errors (SE) are for raw coefficients. Standardized coefficients are based on relevant ranges computed using a query-based approach.

† The shrub all production submodel is a simple calculation from shrub short and shrub tall production and has no r^2.

tending to increase hydric conditions and elevate conservatism. This effect has an unresolved interpretation; however, it may be an important opposing force to the reduction in conservatism from human soil disturbance acting through composite HD. Sixth, historical beaver activity is associated with more hydric conditions, which indirectly elevates conservatism. There are no linkages in our data between conservatism and shrub production, shrub biomass, shrub browse, or ungulate activity.

Effects on degree of invasion

In Fig. 8, we show the predictors and pathways leading to the degree of invasion (see also Fig. 6). There are six direct predictors in the final submodel, accounting for 57% of the variation in the degree of invasion in our data set. A higher degree of invasion is directly and strongly predicted by increasing composite HD, lower elevation, less hydric conditions, increased shrub production, and a riparian or wet meadow wetland type (relative to fens).

There are a total of 18 indirect pathways linking predictors to degree of invasion. All four components of composite HD have indirect effects through HD: Greater hydrologic alteration strongly increases the degree of invasion; increasing anthropogenic soil disturbance increases the degree of invasion; degree of invasion is higher closer to roads; and buffer areas with a higher percentage of natural land cover types and/or less human land use decrease the degree of invasion.

Human disturbance has an indirect negative effect through short or tall shrub production on the degree of invasion opposite of the direct positive relationship between HD and degree of invasion. HD lowers shrub production which, because of the positive relationship between shrub production and invasive species, on balance reduces the degree of invasion. All four components of composite HD have indirect pathways linking them to degree of invasion through HD and short or tall shrub production, suggesting that the positive effects of shrub production on degree of invasion extend to more specific impacts from soil disturbance, roads, human land use in wetland buffers, and hydrologic alterations.

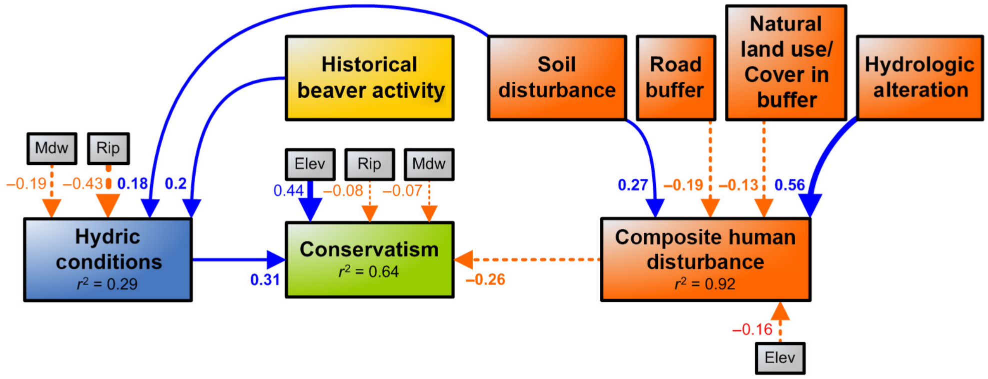

Fig. 7. Specific predictors of conservatism. Variance explanation and standardized effect sizes are also shown. Symbols are as in Fig. 6. Additional details are presented in Table 2.

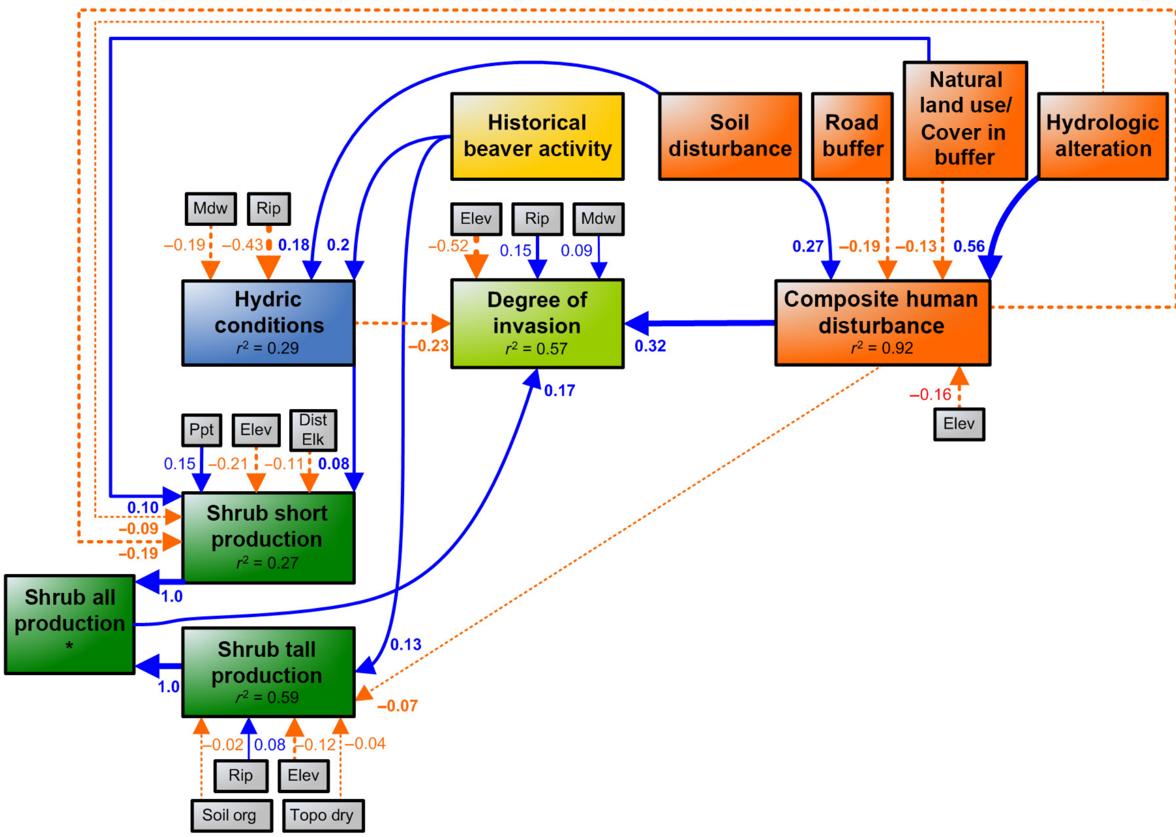

Fig. 8. Specific predictors of degree of invasion. Variance explanation and standardized effect sizes are also shown. Symbols are as in Fig. 6. Additional details are presented in Table 2. The shrub all production submodel is a simple calculation from shrub short and shrub tall production and has no r^2.

Anthropogenic soil disturbance has two complex and indirect pathways to degree of invasion in our data. First, it is associated with increasing hydric conditions and decreased degree of invasion. Second, increased hydric conditions from anthropogenic soil disturbance can elevate short shrub production, which is associated with an increased degree of invasion. The net effects

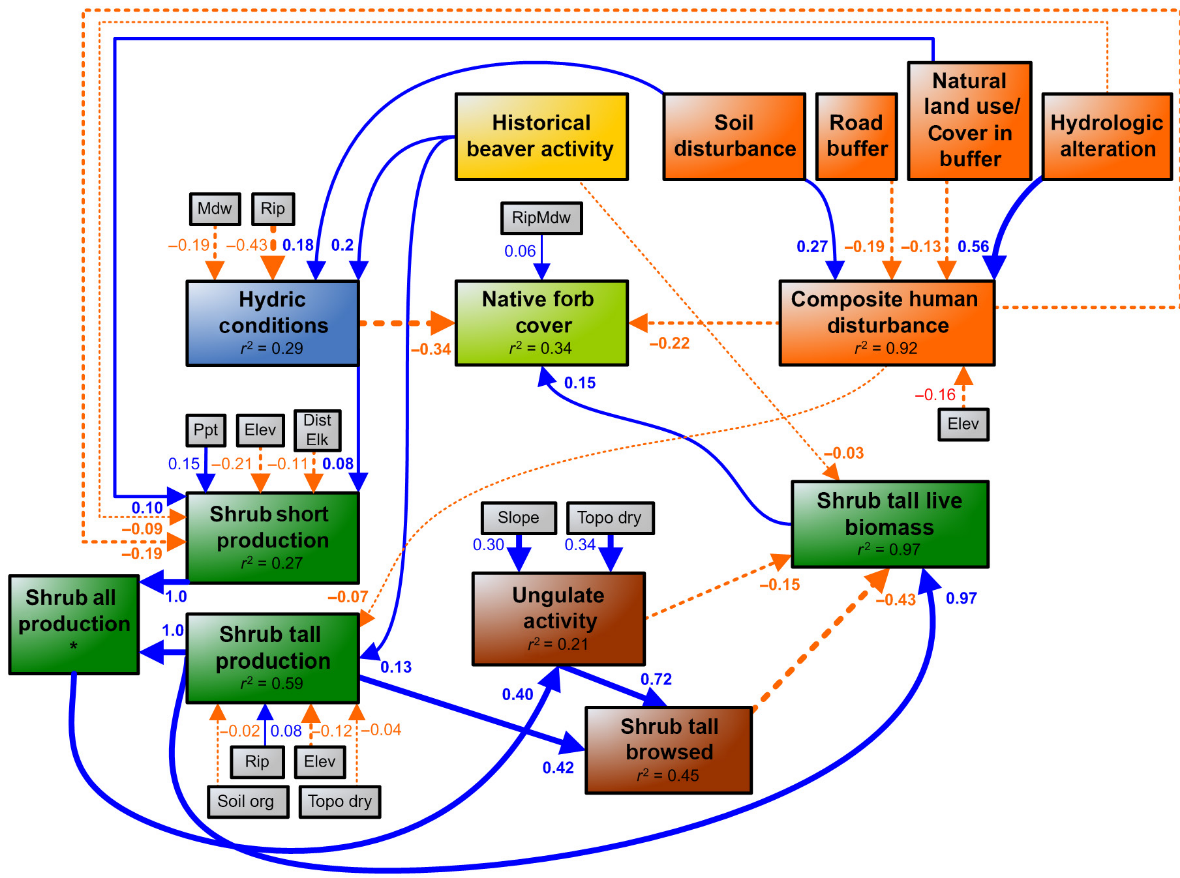

Fig. 9. Specific predictors of native forb cover. Variance explanation and standardized effect sizes are also shown. Symbols are as in Fig. 6. Additional details are presented in Table 2. The shrub all production submodel is a simple calculation from shrub short and shrub tall production and has no r^2.

of these two pathways are opposite one another and will require more research to resolve, especially on how human soil disturbance elevates hydric conditions. However, in general, these pathways suggest that hydrologic regime and shrub production can mediate the tendency of HD to increase the degree of invasion.

Historical beaver activity has three indirect pathways to degree of invasion. First, remnants of historical beaver-created habitat can support persistent hydric site conditions and can be associated with reduced degree of invasion. Second, the positive effect of remnant beaver landforms on hydric conditions may increase shrub production, which is linked to an increased degree of invasion. Third, remnant beaver landforms are often associated directly (i.e., no elevated hydric conditions as an intermediary) with higher shrub production and an increase in the degree of invasion. While the relationships between beaver activity, increased hydric conditions, and elevated shrub production are generally well understood (i.e., Allen 1983, Peinetti et al. 2009, Marshall et al. 2014), the contradictory impacts on degree of invasion from historical beaver habitat modifications as seen in our data will need more research to fully understand. Our model does suggest that elevated shrub productivity can be an important, if subtle and complex, driver of an increased degree of invasion.

Effects on native forb cover

In Fig. 9, we present a focused look at the predictors and pathways influencing native forb cover (compare with Fig. 6). There are four direct predictors in the final submodel, accounting for

34% of the variation in native forb cover in our data set. Increased native forb cover is directly and strongly predicted by decreasing composite HD, less hydric conditions, increased shrub tall biomass, and by riparian or wet meadow wetland type (relative to fens).

There is a complex array of 28 indirect pathways to native forb cover. Many of these have small net effects, but suggest interesting potential connections. First, all four components of composite HD have indirect effects through HD: Increases in hydrologic alterations and increasing anthropogenic soil disturbance decrease native forb cover; it is lower closer to roads, and wetlands with more natural land cover and/or less human land use in their buffers have increased native forb cover.

Composite HD also has indirect negative effects on native forb cover through short or tall shrub production and tall shrub biomass. These pathways may also include ungulate activity and their browse on shrubs. If these nodes are included, the net effect of HD on native forb cover switches to positive, indicating that if shrub consumption is included, elevated HD may actually increase native forb cover. All four components of HD also follow these same routes through HD to shrub production, consumption, and residual biomass. As with HD, when the pathways from more specific stressors include shrub consumption, the net effect of HD on native forb cover is the reverse of the direct pathway.

Our model revealed four indirect routes from anthropogenic soil disturbance to native forb cover that do not include HD. As with the similar connections between soil disturbance, conservatism, and degree of invasion, it is not clear whether these patterns are artifacts in our data and will require future work to resolve. First, increased human soil disturbance is associated with increases in hydric conditions and subsequently a decrease in native forb cover. Next, increased hydric conditions can increase short shrub production, which then has three routes to native forb cover: (1) increases in tall shrub biomass leading to increases in native forb cover (no ungulate predictors involved); (2) increases in tall shrub biomass leading to increased ungulate activity, reducing tall shrub biomass, which then results in a net negative effect on native forb cover; and (3) increases in tall shrub biomass increasing ungulate activity and ungulate browse, reducing tall shrub biomass and native forb cover. These complex indirect pathways have small net effects. However, they again suggest that the effect of HD on native forb cover can be mediated by complex and indirect pathways through other drivers of wetland condition and that ungulate activity and browse may be beneficial for native forb cover.

Historical beaver activity has six complex and indirect pathways to native forb cover. First, remnant beaver dams, canals, and other landforms are associated with more hydric conditions, which tend to reduce native forb cover. Second, remnant beaver habitat modifications directly increase tall shrub production (omitting the connection through hydric conditions), which increases tall shrub biomass and native forb cover. This is the opposite effect of the simpler pathway through only hydric conditions. Third, if this pathway includes the positive response of ungulates to increased shrub production and the negative effect of ungulate activity on tall shrub biomass, the net effect switches to a decrease in native forb cover. Fourth, the third pathway can also include ungulate browse, which still results in a net reduction in native forb cover. Fifth, the first pathway may be expanded to include the positive effect of hydric conditions on short shrub production and the subsequent increase in ungulate activity, which decreases tall live shrub biomass and native forb cover. Finally, the fifth pathway may also include the negative effects of ungulate browse on tall shrub biomass and the reduction in native forb cover.

Clearly, remnant beaver habitat features still play a complex role in the system, even though only a few beavers were in the park at the time of our data collection. This suggests important consequences from any future restoration or natural recolonization of the park. For conservatism and degree of invasion, beaver restoration would likely lead to increased wetland integrity. For native forbs, the pattern is more complex and in some cases beaver's return may marginally reduce wetland integrity.

Discussion

Our general hypothesis of ecosystem processes (Fig. 5) supports the findings of our SE model

(Fig. 6). We found the final SE model to be robust without indications of missing linkages, suggesting that we captured most structure in the RMNP data. Importantly, because our analyses controlled for covariance of key environmental gradients such as elevation and wetland type, patterns between a response and its predictor(s) are statistically independent of covariance with these gradients.

Overall, bioindicators of wetland condition in the park appear to be quite sensitive to HD, groundwater hydrologic regime, and shrub productivity (especially as influenced by ungulate browse and residual standing tall shrub biomass). Beaver, once a keystone species, has important lingering effects, suggesting potentially positive consequences for restoring this species in the park. While our SE model cannot explicitly include data on apex predators because of their long absence, previous research supports the hypothesis that dynamics between elk, moose, and wetland habitat are a consequence of the human-mediated removal of large predators from the park (Singer et al. 2002, Estes et al. 2011, Marshall et al. 2014).

By linking our analyses to a metamodel, we were able to define general expectations independent from the specific relationships in the data set. Through this process, we obtained reasonably good model-data consistency. There are three main caveats to keep in mind, however. First, the final model we present is a data-supported set of hypotheses in need of further validation. It is well understood and axiomatic in SEM that the real test for models is their ability to withstand sequential testing (Fieberg and Johnson 2015). Second, some of the mechanisms that lay behind the relationships described here are hypothetical. Third, we draw inferences from our results that assume the structure of our model is correct. While we can test many via checks of model-data consistency, some elements of interpretation must rely on the reasonableness of assumptions made. Also, some relationships are proxies for underlying mechanism(s) and only changes in the underlying causal processes will actually lead to predicted changes. Future studies should ascertain the degree to which the model presented here remains consistent with data. Of special importance will be the determination of whether changes in the system produced via active restoration are consistent with model predictions.

Despite cautions regarding the need to confirm the implications of our analyses, we feel that our model advances our understanding of drivers of wetland integrity in RMNP and provides a general framework for moving forward. These contributions are particularly critical for the restoration of beaver, determining the role of apex predators, and a continued emphasis of park management favoring resource conservation for future generations in balance with contemporary visitor use. Our results provide a basis for management in an adaptive context (Holling 1978). Management design should accommodate new insight from continued monitoring and future models given that some elements of our results suggest novel connections and/or are based on small coefficients.

Conservatism

Conservatism is a generally useful biometric of wetland condition, both in RMNP and in other landscapes (see Appendix S1; Rocchio 2007*a*, *b*, U.S. EPA 2015). Our SE model supports the expectation that conservative species persist better in habitats with less composite HD. This pattern may be due to the magnitude and accelerated rate at which most anthropogenic disturbance occurs and the inability of conservative species to adapt to these types of changes. Conversely, there appears to be little negative effect of natural disturbances regimes on conservatism in our data, which is quite interesting. Conservative species may be able to respond to the more "evolutionary familiar" pace and extent of natural disturbance regimes. For example, through natural succession, it can often take several decades or longer (Butler 2012) for typical beaver ponds in RMNP to transition into a wet meadow with the fine-textured hydric soils (Westbrook et al. 2011) supportive of conservative species (i.e., silvery sedge, *Carex canescens*). In contrast, human modification can drain or completely replace a wetland in a matter of months (Hyvönen and Nummi 2008, Nummi and Kuuluvainen 2013)—few if any conservative species may accommodate such a rate of change.

Alternatively, it may be the maintenance of high water tables (either from beaver habitat modification or from successful human restoration) that supports conservative taxa. In 2008, the final steps of the restoration of a golf course in Moraine Park (see Fig. 2A) were completed. An earlier restoration to remove an agricultural drainage ditch in Big Meadows was completed in the late 1980s (Cooper 1990, Cooper et al. 1998). These management actions have resulted in beneficially altered hydrologic regimes at both sites and the reestablishment of several obligate and conservative species including cotton grass (*Eriophorum angustifolium*), elephant head lousewort (*Pedicularis groenlandica*), and Aulacomnium moss (*Aulacomnium palustre*).

Shrub production, ungulate activity levels/browsing, and the biomass of tall shrubs had little influence on conservatism in our SE model. This is somewhat surprising given the often strong connections among herbivores, canopy structure, and understory species composition observed in many ecosystems, including wetlands (Augustine et al. 1998, Xiong et al. 2003, Wolf et al. 2007, Kaczynski and Cooper 2015*b*). It may be that conservative wetland taxa are so sensitive to HDs, especially hydrologic alterations, that they have been largely removed from RMNP's low-elevation large valley bottom riparian and wet meadows where the interplay between shrubs and ungulates largely occurs.

Degree of invasion

While protected landscapes might mitigate some effects of plant invasions, the borders of even large parks like RMNP offer little protection in time or space (see Appendix S1; RMNP 2004, Allen et al. 2009). In RMNP, many invasive plants were already present at the time of the park's establishment, particularly European pasture grasses and associated forbs introduced to create hay meadows for domestic livestock and pack stock. Our SE model indicates that high levels of composite HD directly predict a greater degree of invasion in RMNP wetlands. Moreover, anthropogenic soil disturbance, proximity to roads, hydrologic alterations, and reduced natural land cover in wetland buffers all indirectly influence degree of invasion acting through composite HD.

Many invasive species disperse along road corridors (Forman and Alexander 1998), and the proximity of sites to roads may directly influence the potential for a site to be invaded (Al-Chokhachy et al. 2013). Many of our sites near roads do have higher degrees of invasion. However, sites with properly functioning hydrologic regimes may counterbalance this. For example, one of the most intact fens in the park (*Sphagnum* Fen) is immediately adjacent to the main park highway yet its groundwater sources are not negatively influenced by the road grade. As of 2015, *Sphagnum* fen has no invasive species and a higher level of conservatism.

Hydrologic alteration seems to play an especially strong role in influencing invasion. Our hydrologic alterations metric includes several larger-scale attributes such as the total number of diversions in a site's watershed and the percentage of a site's surface water hydrologic network that is upstream of diversion(s). Diversions may reduce surface water flow into wetlands and reduce groundwater recharge (Cooper et al. 2000, Chimner and Cooper 2003, Woods et al. 2006). This may enhance invasion opportunities by exposing more sediment that weeds readily colonize (Tousignant et al. 2010).

Perhaps some of the more nuanced linkages between HD and invasion are the complex indirect connections through hydric conditions and/or shrub productivity. Composite HD is directly associated with decreased productivity of both short and tall shrubs, likely due to residual effects of how many wetlands in the low valley areas of the park were once heavily used for visitor recreation and/or as pasture to support livestock. In turn, the productivity of shrubs may have a direct and positive effect on the prevalence of invasives in wetland vegetation, perhaps because of the potentially complex connection between site productivity and potential species richness (Grace et al. 2016) or the often superior competitive ability of invasive species for limiting resources (Schoener 1983, Tilman 1999). Therefore, the complete indirect path from composite HD (or one of its components) through shrub production to the degree of invasion becomes a negative effect—the reverse of its direct pathway.

Our results also point to a suite of complex pathways linking persistent remnant beaver habitat modifications to both an increased and decreased degree of invasion. Two indirect pathways offer interesting possibilities for thinking about how beaver might, if successfully restored, either improve or complicate the functioning of wetlands in the park (Houlahan and Findlay 2004, Catford et al. 2011). First, persistent historical beaver habitat modifications often maintain hydric conditions decades after beaver abandon a site and these wet conditions support more specialized hydrophytes. With the possible exception of cattail (*Typha* spp.)—rare in the high-elevation wetlands of RMNP—most invasive plants that occur in the park are nonhydrophyte generalists unable to survive in intact wetlands with persistent high water tables. This positive effect of beaver on degree of invasion may counterbalance the increase in weedy plants caused by HD. Second, persistent historical beaver habitat modifications can also directly and indirectly increase shrub production. Beaver are unique herbivores whose complex foraging behavior harvests willow close to the ground, often inducing basal sprouting (Allen 1983, Peinetti et al. 2009, Kaczynski and Cooper 2015*a*). Willow are highly adapted to repeated harvest and when in good condition sprout new basal stems in proportion to the number cut by beaver (Kindschy 1989) and increased net primary productivity (Baker et al. 2012). Our model results suggest that this increase in shrub production can persist long after beavers have abandoned a site. As described above, we see positive associations between enhanced shrub production and degree of invasion in wetlands. While the total effect size of this is small and will require more research to confirm, it does suggest that resource management may need to carefully monitor any possible beaver restoration to determine whether increased shrub production subsequently elevates invasion, potentially counteracting the positive effects of beaver on hydric conditions that reduce the degree of invasion.

In intact ecosystems, with sustainable populations of ungulates (in large part because their apex predators are in place, Coughenour 2002), beaver and willow are often characterized as mutualists (Stachowicz 2001, Bruno et al. 2003). Wetlands in this context might have higher ecological integrity with vegetation characterized by conservative taxa, generally resistant to invasion, and depending somewhat on wetland type, higher cover of native forbs. This has not been the case in many RMNP wetlands for years. Yet, this is the reference condition to which the park aspires and is moving toward through recent management actions (U.S. NPS 2007).

Native forb cover

Native forb cover is our simplest bioindicator computationally, but the most complex in terms of the number of pathways that lead to it in the SE model and in its ecological interpretation. It is also the metric with the greatest variation in response across wetland type and thus may be more difficult to generalize across the diverse RMNP data set or to other systems (see Appendix S1). Nonetheless, native forb cover plays an important role in our story as it responds both directly and indirectly to HD and has several pathways through the natural disturbance loop of the SE model (shrub production, ungulate activity, and shrub biomass, see Fig. 8).

Increased composite HD, elevated HD of soils, decreased distance to roads, less natural buffer areas, and higher hydrologic alterations all reduce native forb cover. Why this occurs will require more study. The pattern is opposite what we see with invasive taxa even though several native forb species can be invasive such as largeleaf avens (*Geum macrophyllum*) and Norwegian cinquefoil (*Potentilla norvegica*). Yet the more important invasive taxa in RMNP are nonnative and the response of native forbs to HD is not likely due to the life history characteristics of invasive taxa. Native forb response to HD is identical in direction and similar in magnitude to the response of conservatism. Many native forbs are conservative species, for example, felwort (*Swertia perennis*) and brook saxifrage (*Micranthes odontoloma*). Yet other native forbs have below-average conservatism (i.e., woodland strawberry [*Fragaria vesca*] or common cow parsnip [*Heracleum sphondylium*]) and occur in sites with combinations of predictors such as minimal human hydrologic alteration and more natural wetland buffers that predict higher levels of conservatism. Therefore, the native forb response is not entirely due to forbs that are invasive or the sensitivity of conservative native forb species to HD.

Some of the negative response in native forb cover to HD(s) may be due to complex indirect pathways involving hydric conditions, shrub productivity, ungulate activity, tall shrub biomass, and remnant beaver habitat modifications.

While statistically small, these include some important interactions that connect HD to native forb response and may be important to consider in restoration efforts. First, when the pathway includes shrub productivity and shrub biomass, composite HD and/or its specific disturbance components have a negative effect on shrub production. Higher shrub productivity (without increased ungulate browse) increases shrub biomass, especially of tall stems. We see a positive response in native forb cover to increased tall shrub biomass (for a specific but representative visual example, compare Fig. 3A with B). Assuming tall shrub biomass equates with higher cover, this may be due to wetland forbs having specific insolation requirements with many species adapted to at least some shade (Keddy 1989, Anderson and Leopold 2002, Battaglia and Sharitz 2006, DeWine and Cooper 2008). Yet, we still see a net negative relationship between HD and native forb cover. Including shrub production and tall biomass in the series of interactions only reduces the magnitude of this effect.

However, increased shrub productivity can attract elk and moose increasing levels of browse (Singer et al. 2002, Dungan et al. 2010). Ungulate herbivory tends to reduce tall shrub biomass and canopy coverage, especially when wetlands lack beaver and their positive effects (Peinetti et al. 2002, Singer et al. 2002, Zeigenfuss et al. 2002). If the pathway includes ungulates and their browse, the relationship between HD and native forb cover becomes positive. While this effect is small, it suggests once again an important role of natural processes in buffering the effects of HD on wetland condition.

As with our other two bioindicators, persistent historical beaver habitat modifications often lead to more hydric conditions. Monocots tend to be more flood tolerant than dicots due to adaptions like hollow stems, adventitious roots, and a lack of woody tissue, all developed during monocots' evolution in aquatic or semiaquatic habitats (Takhtajan 1969). Many native forbs lack these adaptations and have shallow root systems that may require more specific water table conditions (Kercher and Zedler 2004). Our data indicate some nonlinearity between native forb cover and hydric conditions with peak cover values midway along the hydric gradient, especially in riparian sites (see Fig. 4B). Yet, overall native forb cover decreases with increased hydric conditions. Thus, while not quite as simple as the clear benefit to wetland condition that remnant beaver features provide via reducing invasives and elevating conservatism, beavers likely still play an important role in native forb cover via their effects on hydrologic regime.

Implications

To this point, we have focused on the retrospective question of "How did current conditions come about?" Such a focus is the natural product of statistical analyses of survey data. However, we can also pose prospective or forward-looking questions based on the model and results produced.

It is likely that many of the strongest effects of HD on RMNP wetlands are from historical anthropogenic land use. The degree to which these effects are reversible (system recovery simply due to reduced HD) is unknown. Certainly, the past introduction of invasive species is not reversible by limiting further introductions. Rather restoration will require active management focused on the most detrimental species (Wittenberg and Cock 2001, Pimentel et al. 2005, Van Wilgen et al. 2011). Mediated effects from HD to other parts of the system, however, may represent much better avenues for model-predicted interventions. At present, we are reluctant to make these predictions quantitative until further data help evaluate the previously obtained parameters. Qualitatively, however, the model suggests some possibilities.

One of the most important mediators in the system is hydric conditions. The degree to which hydric conditions are altered from historical norms, especially where water tables have declined, is a good predictor of our integrity measures. This is hardly surprising given the many well-documented connections between wetland condition and hydrologic regimes (i.e., Brinson 1993, Cooper et al. 1998, Bedford 1999). It supports direct management of wetland integrity via restoration of hydric conditions. In limited cases, this might be via active restoration of channels and ponds via installed structures and other techniques (i.e., Bilyeu et al. 2008). However, given the wilderness character of the park and the desired reference conditions, this is likely best done through reestablishment of beaver, the habitat they need, and a food web that would allow this species to be once again a functional component of the parks ecosystems. RMNP's Elk and Vegetation Management Plan is currently pursuing many of these avenues for restoration (U.S. NPS 2007). This might create the critical hydric conditions and enhanced shrub production that improves all three of our biometrics and wetland ecological integrity. Of note, this requires that ungulate levels be sustainable such that excessive browse does not switch the positive effect of elevated hydric condition on native forb cover to a negative influence—one of the more subtle and interesting pathways revealed by the SE model. In general, while retrospective analyses indicate that many of the indirect pathways to biotic condition from HD have small coefficients, our model suggests that direct alteration of hydrology can short circuit those long and indirect paths and potentially produce large immediate consequences. Given the strong direct effect of hydrologic regime, we would expect conservatism to increase, invasives to decrease, and native forb cover to increase (perhaps nonlinearly) with restoration of natural hydrologic regimes.

Reducing HD and/or its components might also have positive effects on shrub production. This may cause an unfortunate increase in invasives if weedy species also favor the more productive conditions that reduced human influence may cause in RMNP's wetlands. However, this effect should be small and these invasive species tend to be pasture grasses or relatively naturalized taxa like common dandelion (*Taraxacum officinale*) that are less problematic.

For a variety of reasons, including the implementation of the park's Elk and Vegetation Management Plan (U.S. NPS 2007) populations of elk fell to around 300 animals in 2015 on the eastside winter range, well below the regions carrying capacity (Ketz et al., *in press*). This elk density is similar or lower than what would be expected if apex predators were in the park (Coughenour 2002). While population data are lacking, moose numbers appeared to increase through 2015, perhaps replacing some of the pressure from elk on the park's wetland. Moose eat 5–10 times more willow than elk (Dungan et al. 2010), and thus, their influence is likely exponential, not additive to elk. Data available for our SE model only included up to 2011 so we have not included any effect of these reduced elk numbers and elevated moose numbers. Thus, a useful test of our model will be to incorporate more recent wetland data that track these changes in the relative abundance of elk and moose. Our model would predict increased shrub production, increased tall shrub biomass, and more native forb cover from lower overall ungulate pressure. The park constructed several large ungulate exclosures beginning in 1994 (U.S. NPS 2007), which mimic many of the elements of our model; in particular, exclosures reduce (but do not remove) direct HD and ungulate use. Data from the exclosures soon after they were established suggest higher shrub production, increased tall biomass, and, in many cases, native forb cover (Singer et al. 2002, Zeigenfuss et al. 2002). Observations in 2014 and 2015 suggest that conservatism is higher in the exclosures and the degree of invasion is reduced (E. Schweiger, *unpublished data*).

Conclusions

We conclude by returning to our initial question: "How have HDs altered wetland integrity in RMNP?" The answers to this question may help resource management move beyond bioassessment while also illustrating the benefits of adopting a SEM approach.

Overall, it appears that the "how" behind the loss of integrity in RMNP's wetlands is largely a historical HD story, overlain by the variance in the abundance of elk and moose, causing the loss of beaver and nearly eliminating the once-dominant tall willow communities. Low-elevation portions of the park are surprisingly disturbed hydrologically for a large protected wilderness. Many of these disturbances are legacy effects from alterations that occurred before the park was formed and prior to park management's shift to a focus on ecological integrity. These have the largest impacts in large valley bottom wetland complexes, where the cumulative effects of missing beaver, historically large ungulate herds, as well as historical visitor use and visitor facilities coincide. Most of the remote, small wetlands in the park remain intact (see Appendix S1) and are well protected by current park resource management strategies (U.S. NPS 2007). Yet some disturbances, like the

Grand Ditch, are grandfathered into legislation, still operate, and influence the integrity of park ecosystems. Other research has reached some of these same conclusions (i.e., Singer et al. 2002), yet we are able to quantify the role of HD in a novel way with the SE model, describing many of the interactions in the park in a structural or causal sense. We developed our models from a variable-rich data set that spans three major wetland types and multiple environmental gradients in the park. This helps focus our efforts on the most important drivers and better understand responses. For a wilderness park like RMNP where competing values of ecological integrity, wilderness character, and visitor services all vie for limited resources, our results have important implications. This may be especially relevant as we enter into a period of unprecedented uncertainty due to climate change.

As we note in several places above, apex predators are often key components in similar wetland ecosystems where large herbivore- and beaver-controlled hydrologic processes are critical. Our metamodel hypothesizes that the trophic downgrading of the park is in part responsible for the loss of wetland integrity in RMNP. Should wolves ever return to the park, this will present a real sequential test for our model (Fieberg and Johnson 2015); in the interim, implementation of the Elk and Vegetation Management Plan (U.S. NPS 2007) serves as a surrogate.

Through the exploration of connections between HD and wetland bioindicators, we hope to have furthered our understanding of wetlands in RMNP and illustrated that monitoring data are often underutilized. Conventional approaches to statistical analysis are characteristically reductionist, seeking to isolate individual effects and/or describe net effects (see historical discussion in Grace 2015). However, the needs of science and society call for us to move to more integrative models of causal networks of relationships. They also call for a capacity to step down our general understanding so as to provide a better understanding of place-based ecology (sensu Billick and Price 2010). Place-based ecology, with an understanding of its environmental history, provides improved local understanding of ecosystem behavior that provides managers the opportunity to better adapt to new knowledge and ultimately restore resilient landscapes. Long-term ecological monitoring such as conducted by the Inventory and Monitoring Program of the NPS can help in the understanding of place-based ecology in some detail by facilitating both the discovery and extrapolation of system structure. Here, we have illustrated an approach to this aspiration that we believe can have wide applicability in natural resource management.

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Supporting Information

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